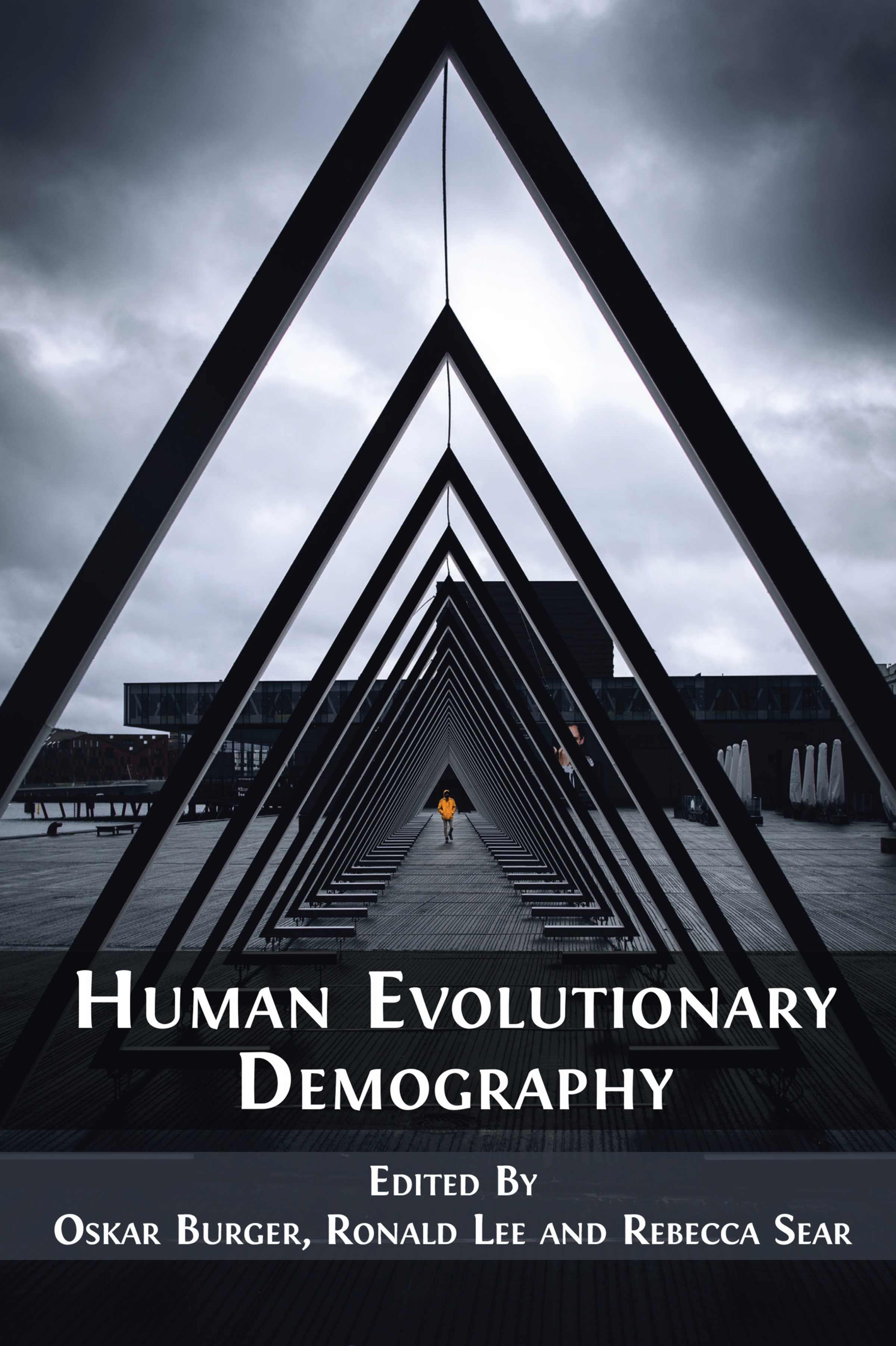

HUMAN EVOLUTIONARY DEMOGRAPHY

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6. Ecological Evolutionary Demography: Understanding Variation in Demographic Behaviour

Siobhán M. Cully & Mary K. Shenk

Ecological evolutionary demography is the branch of evolutionary demography that focuses on the potential adaptive value of demographic behaviour at the level of the individual. First defined by Low and colleagues some twenty-five years ago, ecological evolutionary demography has gained important ground in developing our understanding of the ultimate evolutionary ecological drivers of fertility and mortality, often in combination with more proximate determinants of these demographic outcomes. In doing so, the field has provided solutions for apparent paradoxes associated with human fertility — how humans sustain high fertility despite highly dependent young and slow development of offspring, as well as the demographic transition — and has led to an improved understanding of the basic pattern of human mortality. A third core area in mainstream demography — migration — has received less attention from an ecological evolutionary perspective, but work on dispersal generates insights into how various "push" and "pull" factors affect the costs and benefits of leaving the natal community, and how such strategies vary across individuals, households and societies. Given the broad framework underlying ecological evolutionary demography investigations of demographic behaviour, the field has outstanding potential for integration across demography and the evolutionary social sciences. We offer several potential pathways for immediate pursuit and anticipate that this will invigorate further the impact of the field on understanding human demographic behaviour.

Introduction

> Demography lies at the heart of every statement about selection.
>
> — Jones (2010, p. 74)

Biological, anthropological and formal demographers have long pursued a set of overlapping interests in parallel and with limited interchange. This is despite clear overlap in goals and methods: demography's core concepts of fertility and mortality are central to the definition of biological fitness that serves as the foundation of the evolutionary sciences (Jones, 2010) and evolution has provided much-needed theory for the primarily descriptive discipline of population demography (Kaplan and Gurven, 2008; Sear, 2016).

"Ecological evolutionary demography" (EED) (*sensu* Low, Clarke, and Lockridge, 1992) represents a marriage of these interests. It is the study of contemporary human demographic

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behaviour from an evolutionary and ecological perspective. With its origins in the fields of evolutionary and behavioural ecology, ecological evolutionary demography focuses equally (1) on how individual demographic behaviours adjust to particular socio-ecological contexts both historically and cross-culturally, and (2) how individual-level constraints affect decision-making *within* a given socio-ecological context (Smith and Winterhalder, 1992a). In particular, ecological evolutionary demography anticipates that individuals will adjust their (demographic) behaviour in the pursuit of maximizing lifetime reproductive success[1] (LRS) such that, consciously or unconsciously, an individual makes decisions that attempt to maximize fitness.[2] EED is distinct from the broader discipline of human behavioural/evolutionary ecology in its explicit interest in demographic outcomes: fertility, mortality and migration. EED overlaps with other areas of evolutionary demography, but is distinct from mainstream evolutionary demography due to its strong empirical focus on using data from (relatively) contemporary populations to: (1) understand the evolution of species-typical traits (e.g. the human mortality profile); (2) test evolutionary hypotheses about demographic traits; and (3) to understand variation in contemporary demographic patterns.

The evolutionary ecological view of human demography thus has been largely divorced not only from mainstream, medical and anthropological demography, but also from much research in the field of evolutionary demography as practised by evolutionary biologists whose work generally focuses on non-human species. For example, although both sets of scholars refer to themselves as "evolutionary demographers", ecological evolutionary demographers studying human demographic behaviour — generally from interview, survey or historical data — make up a small fraction of the evolutionary demography society,[3] the primary academic society supporting scholarship in evolutionary demography. Instead, many evolutionary demographers focus more heavily on the evolutionary biology of life history trade-offs, with a particularly strong emphasis on understanding the limits to lifespan (e.g. Carey, 2003; Zuo and others, 2018; Colchero and others, 2016; Dong and others, 2016), and how longevity trades off with fertility (e.g. Kirkwood and Rose, 1991; Gagnon and others, 2009; Bolund and others, 2016), generally with a stronger focus on animal and plant models and experimental — as opposed to observational — methods.

Chapter Outline and Objectives

In the remainder of this chapter, we hope to clarify both the particular contributions made by ecological evolutionary demographers to the broader field of evolutionary demography, and the scope for increasing integration of the EED perspective within core areas of evolutionary demography. This chapter is modelled on Low et al. (1992), and aims to provide a broad, if not comprehensive, overview of EED as it has informed understanding of core demographic concerns: fertility, mortality and migration. In each area, we synthesize recent and seminal theories and case studies and show how these provide new and important insights into the

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[1] More recently, and in light of worldwide demographic transitions, ecological demographers have begun to explore proxies — especially status — for LRS as ultimate motivators for demographic behaviour (see e.g. Kaplan, 1996; Mattison and Sear, 2016).

[2] By fitness, we do not mean fertility. While fertility is sometimes used as a proxy for fitness, as discussed, pursuing maximum fertility often does not maximize fitness.

[3] https://evodemovi.weebly.com

ultimate drivers of demographic behaviour. These sections are flanked by an expanded discussion of the theoretical and methodological toolkits used by EED and a conclusion that notes how EED is poised to contribute to our understanding of complex demographic behaviour within and across societies. While obviously relevant, ecological drivers of demographic behaviour, per se, are not central to this chapter; these are reviewed usefully by Uggla (this volume).

Core Frameworks, Methods and Datasets

Ecological evolutionary demography uses core principles from the field of human evolutionary and behavioural ecology, notably life history theory, to understand the ultimate causes of demographic behaviour. The goal of life history theory is to explain the evolution and development of strategies that optimize the usage of resources across the life course and across varying ecological conditions (Stearns 1992). Life history strategies exist at the species level as responses to past ecological conditions and at the individual level as responses to variable ecological and developmental conditions (Ellis and others, 2009). According to this framework, demographic behaviour is the outcome of allocation decisions whereby an individual chooses how to invest energy and resources across a number of competing biological demands, including somatic effort (growth, maintenance of the body, immune function) and reproductive effort (mating and parenting). Variation in life history traits such as age at sexual maturity, age at first birth, birth spacing, age at last birth, and number of offspring born, results from trade-offs in the distribution of resources or energy to these competing life functions (Stearns, 1992; Charnov, 1993; Roff, 1993). The "principle of allocation" contends that greater investment in one domain — growth, maintenance, mating, gestation, parenting — occurs at the expense of others. The costs and benefits of different strategies and trade-offs vary as a function of individual characteristics (e.g. age, sex, health status) and local circumstances (e.g. resource distribution, level of competition for mates or resources), meaning that strategies that are optimal for an individual in one environment are not optimal for a different individual in a different environment (Ellis et al., 2009; Bogin, 2009; Chisholm, 1999; Hill, this volume).

There are several aspects of the ecological evolutionary approach that complement mainstream demographic approaches. First, whereas mainstream demography is primarily "bottom-up" — building theory from observed associations — ecological evolutionary demography is primarily "top-down" — testing well-developed theories with demographic data (Kaplan and Gurven, 2008). In essence, ecological evolutionary demography tends to pursue what Ernst Mayr and then Niko Tinbergen (Mayr, 1961; Tinbergen, 1963) referred to as "ultimate" questions, surrounding the fitness value of traits in contemporary environments, whereas mainstream demographers are typically more interested in "proximate" questions, examining the correlates and predictors of patterns of demographic behaviour, often without asking why or how the behaviours benefit or disadvantage the individuals who perform them (Low and others, 1992: 5). Importantly, proximate responses to environmental factors that affect demographic behaviour will not be maintained if they are not favoured by selection. Thus, in our view, a complete understanding of demographic behaviour requires an evolutionary perspective, as this perspective is the most likely to provide information about the stability of observed associations over time and across contexts.

Second, ecological evolutionary demography focuses strongly on individual decision-making within specific contexts — employing "methodological individualism"[4] (Weber, 1978; Smith and Winterhalder, 1992a) to make inferences about how an individual's characteristics lead to optimal behaviour that is specific to that individual. Mainstream demography has historically made greater use of data aggregated at larger levels (e.g. cities, countries or other populations) to make inferences about how social and economic variables affect demographic behaviour at regional scales. A focus on the individual level is well represented in recent work in demography (a tradition known in the field as "microdemography"), but has tended to emphasize quantification of, proximate causes for, and/or policy-relevant aspects of demographic events. This difference in approach affects how the costs and benefits of demographic behaviour are understood (Low and others, 1992: 11). In particular, benefits at the societal level may be directly contradicted by individual-level benefits. For example, encouraging fertility reduction (e.g. see Bulatao, 1985) is very unlikely to be successful if such behaviour is promoted to "benefit society" and more likely to be successful if it is accompanied by tangible benefits to parents of fewer children. Daughter-neglect is similarly resistant to "public good" incentives; a variety of examples suggest that the valuation of daughters arises in relation to the perceived usefulness of those daughters to individual families (e.g. Das Gupta and others, 2003; Fraser Schoen, 2014). Indeed, EED is explicitly interested in how *variation* in demographic behaviour arises and is sceptical of inferences drawn from pooled data that compare *central tendencies* due to the problem of overextending inferences caused by the ecological fallacy[5] (Pollet and others, 2014), and the potential to obscure underlying causes of demographic behaviour that are driven by individual-, not population-level considerations (e.g. Alvergne and Lummaa, 2014; Low, 2000).

Third, ecological evolutionary demography is especially concerned with the ways in which the specific socio-ecological contexts in which individuals are embedded modify individual demographic behaviour (see also Uggla, this volume). EED employs "ecological selectionism"[6] — under the assumption that different ecologies are likely to produce different behavioural optima. For example, different types of subsistence systems correlate with different demographic behaviours in terms of age of marriage, number of marriage partners and level of fertility both across and often within societies. Across populations, horticultural societies, which are limited in terms of the labour needed to work the land ("labour-limited"), are commonly polygynous with relatively early ages at first marriage (Goody, 1976; Harrell, 1997), while intensive agricultural societies, where resources are limited by the amount of land available ("land-limited"), are more likely to be monogamous and focus investment on a smaller number of offspring. Within-society variation is leveraged by Daniel Nettle to explore how environmental harshness in contemporary England maps onto reproductive behaviour. He finds that individuals residing in deprived neighbourhoods have faster life histories,

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[4] Methodological individualism "holds that properties of groups [...] are a result of the actions of its individual members". (Smith and Winterhalder, 1992b). We use it here to emphasize that EED is primarily interested in variation in demographic behaviour at the individual, rather than group, level.

[5] The ecological fallacy refers to incorrect inferences made by assuming relationships observed at the aggregate level represent individual-level processes (Pollet and others, 2014).

[6] "Ecological selectionism" asks "What are the ecological forces that select for behavior X?" (Smith, 2000) and thus anticipates behaviours being shaped differently by different environments or socio-ecological contexts.

reproduce earlier, more often and with lesser apparent investment in each child (Nettle, 2010). There is also increasing attention being paid to understanding the effects of ecological context at multiple levels within and across communities: Mattison et al. (2022), for example, show that indicators of market integration differ across individual, household and community levels, each with different influences on reproductive and health outcomes.

Finally, while a key strength of ecological evolutionary demography is the focus on empirical work in contemporary or recent historical populations, researchers have also borrowed formal models from economics (e.g. Kaplan, 1996), population genetics (e.g. Coulson and others, 2010), and formal demography (e.g. Jones and Bliege Bird, 2014; Rogers, 1990) to draw conclusions about demographic behaviour. An exciting recent development has been the increasing incorporation of models from cultural evolutionary theory (e.g. Mattison et al., 2018; Kolodny, Feldman, and Creanza, 2018), such that demographic behaviour is predicted not solely on the basis of what behaviours are predicted to be optimal, but also on the basis of how behaviours are socially transmitted. Although the attempt to integrate these disciplines is in its early stages (Creanza and others, 2017), demographic behaviour (as opposed to demographic intent) is readily observed and may provide one of the more straightforward routes forward for refined synthesis. This line of thinking should also address with much more clarity the extent to which cultural processes may be ultimately responsible for demographic behaviour, as commonly assumed by demographic models (Low and others, 1992: 8), versus the extent to which "materialist" incentives drive demographic behaviour (Sheehan and others, 2018; Shenk and others, 2013) in line with much thinking in human behavioural ecology, versus how these two "forces" interact to drive demographic behaviour (Henrich, 2004).

Methods & Data

Congruent with its focus on the individual, ecological evolutionary demography relies primarily on datasets that include details of individuals' demographic behaviour as the behaviour manifests within particular contexts (i.e. the household and the local community). The earliest examples derive from first-hand data collection in small-scale communities, whose demographic behaviour, by "ethnographic analogy",[7] could provide unique insights into presumed behaviour of prehistoric human ancestors. James Woodburn was an early pioneer of such work with the Hadza (Woodburn, 1968; Konner, 2017); his work on the Hadza subsequently inspired numerous demographic inquiries from a "neo-Darwinian" perspective focusing on small-scale societies, including Lee and DeVore's seminal work *Man the Hunter* (1968). Nancy Howell's *Demography of the Dobe !Kung* (1979) "set the standard for hunter-gatherer demography" (Konner, 2017). This tradition has continued in more recent examples, including Frank Marlowe's *The Hadza* (2010), and Nicholas Blurton-Jones' *Demography and Evolutionary Ecology of Hadza Hunter-Gatherers* (2016). Other important works in the EED tradition include Pennington and Harpending's *Structure of an African Pastoralist Community* (1993) and Hill and Hurtado's *Ache Life History* (1996). In each case, the authors

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[7] "Ethnographic analogy" is used to project the behavior of such small-scale communities into the distant past, because such populations are thought to be similar to Pleistocene ancestors given the continuity of selective environments (e.g. Marlowe 2005).

have painstakingly gathered data on the demographic statuses and events experienced by individuals, including births, deaths, marriages and divorces, as well as genealogies that allow these individuals to be linked together in families and lineages. Unlike much of the data gathered in mainstream demographic work, ecological evolutionary demographers often spend years residing within their study communities, so that the data provided is of exceptionally high quality. Indeed, many contemporary methods to circumvent problems of estimating demographic events that arise in non-literate populations were pioneered by ecological evolutionary demographers (e.g. see Konigsberg and Frankenberg, 1992; Quinlan and Hagen, 2008).

A variety of secondary data sets have also propelled ecological evolutionary demography into arguably more complex social realms. These data sets are collected by individuals and groups for different purposes (Smith and others, 2011), but contain data that may be used to reconstruct individual life histories and demographic behaviour. Increasingly used by human behavioural ecologists and evolutionary demographers (Nettle and others, 2013), such data sets provide a number of specific challenges and opportunities that both expand and constrain their use in tests of evolutionarily informed hypotheses.

Common sources for secondary datasets analysed by ecological evolutionary demographers include parish records, household registers and research-driven demographic and public health data sets. Firstly, historical demographic records have been employed successfully by several ecological evolutionary demographers. Such records are invaluable for linking families across multiple generations, within specific, known historical, demographic and ecological contexts, and for detailing the variation in demographic decision-making as it relates to individual constraints and opportunities. Indeed, many of the topics of interest to human behavioural ecologists, such as choice of marriage partner, fertility and mortality schedules, evidence of parental investment and reproductive success (Smith, 2000; Smith and Winterhalder, 1992a), can be examined using data contained in parish registers, allowing for sophisticated evolutionary analysis of pre-existing data in well-described historical contexts (Boone, 1986, 1988; Voland, 2000; Lummaa, 2004; Clarke and Low, 2001).

Secondly, large, statistically robust data sets, including high-quality data on many variables of interest to evolutionary demographers, and derived from large-scale populations, are readily available and often financially cost-free to analyse. These data sets have a number of advantages compared to small primary data sets historically of interest to ecological evolutionary demographers, including large sample sizes, rich data and often longitudinal designs (Mattison and Sear, 2016) that facilitate in-depth analysis of individual life histories. They also point to significant variability within so-called WEIRD (Western Educated Industrialized Rich and Democratic) societies (Henrich and others, 2010) — variability that may be usefully mined to explore the context-specific nature of demographic behaviour in contemporary, industrialized settings (see Stulp and others, 2016).

Yet secondary data sets are subject to a number of important methodological challenges. Firstly, demographic events are often recorded long after they occurred and are subject to errors, including those due to systematic biases in recall (e.g. a propensity to forget deaths of certain classes of individuals, such as the unbaptized). There are techniques to estimate the level of under-registration that is produced by such problems (e.g. Eriksson and others, 2018) and to infer missing data (e.g. Langkamp and others, 2010). Nonetheless, care must be taken to ensure that data are reliable for analysis (see e.g. Wrigley, 1997). Secondly, the population that is able to be registered (i.e. that is "under observation") may differ systematically from the populations about which the dataset serves to generalize. The characteristics and behaviours of migrants may differ systematically from those of individuals who remain in the study area, for example. This can make it difficult to characterize the constraints affecting different classes of individuals and, in turn, how these affect reproductive and demographic decision-making (e.g. Strassman and Clarke, 1998) and the timing of demographic events (Voland, 2000). Thirdly, because secondary data sets are compiled for a variety of different reasons, the ability to use them to examine the complex causal factors affecting individual decision-making can be limited. Reliable socio-economic information is often lacking from parish and household registers, for example, confounding attempts to describe resource-based differences that are often thought to play key roles in demographic behaviour. Large-scale secondary datasets will only have the variables deemed of interest by previous researchers, regardless of whether these are the most relevant variables for any particular analysis (e.g. Shenk and others, 2013). Fourthly, large-scale secondary data sets leave researchers with many "degrees of freedom" (Stulp and others, 2016) that affect how they operationalize variables and conduct analyses and hence draw their conclusions (e.g. Silberzahn and Uhlmann, 2015). Pre-registering protocols may decrease unintentional researcher biases (Munafò and others, 2017), but caution must be exercised assiduously to maintain objectivity. Finally, cross-cultural comparative data analysis has produced exciting results that underscore both the general and context-specific nature of demographic behaviour (e.g. Borgerhoff Mulder and others, 2009; Hill and others, 2011), but poses special difficulties due to the differences in how data were collected or studies deployed across populations. None of these difficulties applies only in relation to work in EED, and all, in our view, are outweighed by the usefulness of inferences that can generally be drawn from appropriate analyses of rich datasets (see also Stulp and others, 2016).

Fertility

Fertility, survivorship and population growth rates together define an individual's fitness. Thus, it is not surprising that fertility has been a key focus of ecological evolutionary demography at least since the 1980s (Sear and others, 2016). In that time, ecological evolutionary demographers have shed light on two key paradoxes: how humans sustain high fertility despite the high costs of childbearing, and why fertility has dropped in industrialized settings in association with the so-called "demographic transition". In addition, the field has contributed theoretical and empirical advances for every component of fertility, from understanding the variation in age at first reproduction, to understanding the predictors of fertility, to predicting interbirth intervals and parity progression, to characterizing variation in age at last birth and explaining menopause. We focus here on some of the key contributions of ecological evolutionary demographers to illustrate the breadth and promise of the field.

The Paradox of "High" Fertility

Evolutionary scholars consider the species-typical fertility of humans to be paradoxically high.[8] Despite the high costs of fertility to human females given extreme altriciality of human infants, human women have faster rates of reproduction than predicted based on non-human primate models (including those of the great apes), and the duration of breastfeeding for our highly dependent offspring is correspondingly short (e.g. Kramer, 2005; Sellen, 2001) (Figure 1). The highest population fertility on record belongs to the Hutterites, a North American Anabaptist sect, whose population reached a total fertility rate of eleven children (Eaton and Mayer, 1953) while the record fertility for an individual woman was set in the eighteenth century by a woman who reportedly gave birth to sixty-nine children (Glenday, 1988). Such figures are remarkable given how dependent human infants are — with brains three times larger than that of a chimpanzee (Navarrete and others, 2011), the energetic demands of human infants are superlative (Walker and others, 2008; Foley and Lee, 1991; Kuzawa and others, 2014). Early in the infant's life, the vast majority of calories provided to feed these demands derives from breastmilk (Sellen, 2007), seriously constraining a woman's ability to meet her own energetic demands alongside those of her young infant, not to mention other dependent offspring at older ages (Gurven and Walker, 2006).

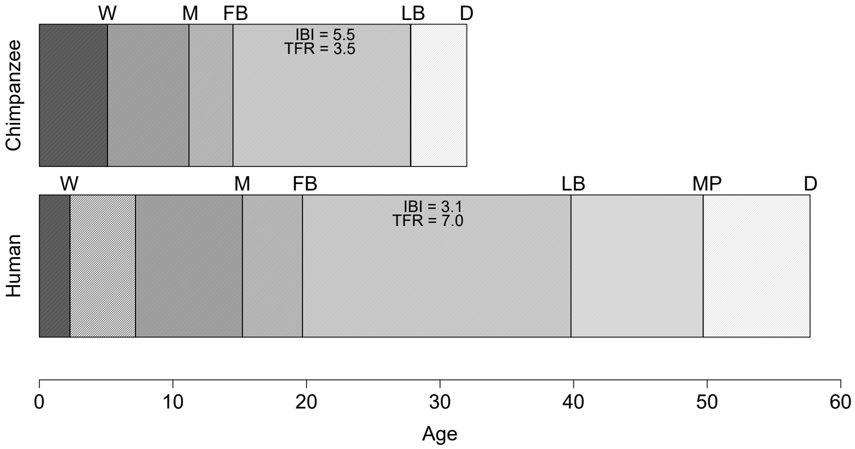

Figure 1. Life histories in chimpanzees (top) and humans (bottom). Human life histories are longer for virtually every distinct phase therein. However, human weaning occurs earlier than expected based on non-human primate models; inter-birth intervals are correspondingly short. W=weaning; M=1st menses; FB=1st birth; LB=last birth; D=death; IBI=inter-birth interval; TFR=total fertility rate. Adapted from Kramer, 2005.

The solution to this, of course, is that human mothers receive significant assistance from others ("allocaregivers"), who subsidize the high costs of child-rearing. Indeed, humans are often

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[8] This is in contrast to mainstream biodemography, which anticipates even higher rates of fertility, given the apparent physiological capacity to reproduce more (e.g., Bongaarts, 1975). We take this up again in describing new questions around the age at last birth.

considered “cooperative breeders” (e.g. Kramer, 2005, 2010; Mace and Sear, 2005; Sear and Coall, 2011; Hrdy, 2005), which implies that assistance in child-rearing is a key feature of the human life history. *Who* provides the most such assistance is debated. The longest-held view is that men form pair bonds with women and, in exchange for female fidelity, take up a provisioning role for their mutual children (e.g. Lancaster and Lancaster, 1987; Kaplan and others, 2000; see Mattison, 2016). This view has been challenged by proponents of the “grandmother hypothesis” (Hawkes, 2004), which posits a larger role taken by maternal grandmothers in caring for dependent offspring, together with evidence suggesting that a variety of other caretakers, including siblings (Kramer, 2005; Turke,1988; Mattison and Neill, 2013), step in at different times and places (Sear and Mace, 2008). We follow Sear (2016a) in emphasizing that while the solution to this paradox involves a *universal* tendency to assist mothers, *flexibility* in humans allows specific caretakers to assist in different contexts.

The Paradox of ‘Low’ Fertility

Evolutionarily high fertility in humans gives rise to the second paradox addressed usefully by ecological evolutionary demography: the demographic transition, a global phenomenon in which high fertility and mortality rates declined to low levels beginning in late-eighteenth-century Europe followed eventually by much of the remaining world. While most scholars link demographic transitions to economic, social and technological changes associated with industrialization and economic development, the specific causal mechanisms most important in transitions remain the subject of debate. Vining (1986) famously argued that “the” demographic transition contradicted evolutionary explanations for fertility given that (a) individuals voluntarily limited their fertility significantly despite increasing access to resources, and (b) wealthy and high-status people often lowered their fertility to a greater degree than people with fewer resources. Since Vining’s paper was published, numerous human evolutionary demographers taking an ecological approach have tackled the question of why the demographic transition has occurred — especially why fertility has declined — and how fertility decline is consistent with evolutionary explanations.

In the broadest sense, evolutionary models of the demographic transition fall into three categories (Borgerhoff Mulder 1998): (i) some argue that the transition is optimal with respect to fitness; (ii) some that lower fertility is the consequence of Darwinian but non-genetic means of inheritance (e.g. cultural evolution); and finally, (iii) some argue that such behaviour is maladaptive.

Causal explanations in ecological evolutionary demography (i.e. (i) above) fall into several categories, which are not mutually exclusive (despite occasional claims to the contrary) — many of which align closely with approaches taken by non-evolutionary demographers (see Shenk and others, 2013 for review). Many researchers taking a life history approach have argued that reductions in rates of risk and mortality — particularly infant and child mortality — change levels of optimal fertility, motivating parents to have fewer children and invest more in each given the greater likelihood that their children will survive and reproduce (e.g. Chisholm and others, 1993; Leslie and Winterhalder, 2002; Quinlan, 2006). Other researchers examine the costs and benefits of investing in self and children. Specifically, when the costs of children are low (for instance when children’s agricultural labour helps to subsidize the costs of their upbringing), fertility should be higher than when the costs of children are high (for example, where land saturation tightly limits inheritance or in modern market economies where children are not economically productive but are costly to raise) (e.g. Kramer, 2005; Mace, 1998; Sear and Coall, 2011; Luttbeg and others, 2000). Kaplan (1996), following Becker (1993), has argued that fertility declines with increasing payoffs to investment in human capital (primarily education) in modern labour markets; these effects may be complemented by increases in adult life span and child survival rates, which also result in greater payoffs to investments in self and in children given the length of time over which benefits accrue (Cervellati and Sunde, 2005; Galor, 2012). The opportunity costs of raising children also increase in modern labour markets, especially for women (Low and others, 1992; Turke, 1989), who may reduce fertility to pursue career opportunities or otherwise delay reproduction to an age when infertility becomes more likely (Kaplan and others, 2000).

Cultural evolutionary theory (ii, above) focuses on the social processes that lead to fertility decline, arguing that humans have evolved learning biases that may lead to (or at least intensify) low fertility through emulation of high-status individuals with few children (e.g. Boyd and Richerson, 1995; Richerson and Boyd, 2005). Related models suggest that in modern societies, the decreasing density of pronatalist kin leads to increasing transmission of low-fertility norms (Newson and others, 2005). Cultural transmission models can be seen either as mechanisms of how fertility decline spreads or as causal models that posit why individuals adopt low fertility — in the former sense they are not “ecological” approaches, but in the latter sense they are.

Increased wealth does not imply a quality-quantity trade-off: Although a quality-quantity trade-off is one way to explain the demographic transition, wealth does not automatically give rise to such a trade-off. In other words, greater wealth (or maternal quality; see Emery Thompson and others, 2016; Ellison, 2003) should not, on its own, produce a fitness advantage through a reduction in childbearing. As encapsulated by Kaplan’s (1996) embodied capital theory, wealth, *per se*, is not what drives investments into child quality over quantity. Rather, socio-ecological contexts that provide sufficient benefits to skills acquisition or other investments in child quality are what set the stage for steeper quantity-quality trade-offs. Because the wealthy tend to inhabit contexts that reward investments in child quality (i.e. wealth and perceived returns to parental investment often covary (Mace, 2008; Lawson and Mace, 2011)), it often appears as though humans violate the more general expectation that wealth *alleviates* the quantity-quality trade-off (Low and others, 2002; Hopcroft, 2006). If so, looking at the relationship between wealth and fertility *within* groups experiencing the same strength of fertility trade-offs should unmask a positive association between wealth and fertility that is not apparent when one does not control for the socio-ecological context producing this trade-off (Mace, 2008) (Figure 2). Few studies have attempted such a multi-level approach, but Alvergne and Lummaa (2014) found evidence both for and against an ecological fallacy applied to wealth and fertility in Mongolia — on the one hand, once context (here, urban versus rural) was accounted for, wealth showed a positive relationship with lifetime reproductive success; on the other, women’s education traded off steeply with childbearing, suggesting that status acquisition could drive fertility to below-optimal levels (see also Shenk and others, 2016). Future work assessing fertility trade-offs must therefore be attentive to how the context establishes returns on investments in child quality and how individual attempts to secure status trade off with investments in posterity.

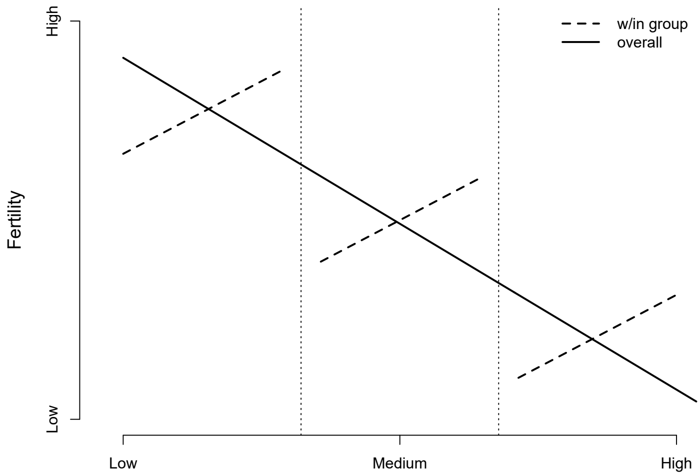

Figure 2. The ecological fallacy and the demographic transition. Data aggregated across contexts may obscure or reverse positive relationships between wealth and fertility that arise within wealth strata.

Timing of Fertility

The historical focus on overall fertility is complemented by a more recent focus on the timing of fertility, including the timing of age at first birth, interbirth intervals and, even more recently, the age at last birth. Timing of reproduction is increasingly recognized as an important contribution to fitness, particularly because fertility poorly predicts fitness in non-stationary populations (Jones and Bliege Bird, 2014). All else being equal, in growing or stationary populations, earlier reproduction is favoured (Voland, 1998): earlier-born offspring represent a greater marginal benefit to parental reproductive success than later-born offspring; and earlier reproduction shortens generation times, increasing fitness over many generations (Lewontin, 1965; Jones, 2011). At the same time, earlier reproduction reflects a key transition in a woman's life history from investments in growth to investments in reproduction (Stearns, 1992; Allal and others, 2004). The timing of this shift is important to future reproductive success, as a woman draws from the reserves built up during the pre-reproductive period to support reproduction after growth has halted (e.g. Hill and Hurtado, 1996). Accordingly, reproduction that occurs too early is associated with poor consequences for mothers and children, including low birthweight (Koniak-Griffin and Turner-Pluta, 2001), whereas greater investments into growth are associated with better outcomes, such as reduced stillbirths and infant mortality (e.g. Sear and others, 2004). In general, organisms should benefit from earlier reproduction if there are no associated costs (see Brown and Sibly, 2006), but should delay reproduction when this improves future reproductive prospects.

Trade-offs in the timing of reproduction arise across the reproductive lifespan, affecting each bout of reproduction (see Sheppard and Coall, this volume). Thus, in addition to age at first birth, trade-offs have been invoked to explain the spacing of births (Blurton-Jones, 1986) and, more recently, the timing of age at last birth (Mattison et al., 2018; Towner, Nenko, and Walton, 2016). In general, longer interbirth intervals are interpreted to reflect increased parental investment in children (e.g, Blurton-Jones, 1986; Bereczkei and others, 2000) and as a means of protecting mothers from the physiological and energetic costs of overly rapid reproduction (e.g. Panter-Brick, 1991). Birth spacing is also a useful nexus for investigating parent-offspring conflict (Trivers, 1974) as children are wont to demand more investment from their parents than is optimal vis-à-vis parental fertility (McDade, 2001; Kushnick, 2009). As with timing of age at first birth, costs and benefits of early versus late reproduction vary according to individual circumstances, and increased availability of resources (e.g. energetic, temporal, financial) are anticipated to alleviate the costs of reproduction and to sustain faster rates of reproduction, all else being equal (Gurven and others, 2016). Unlike age at *first* birth, subsequent births may be less likely to reflect trade-offs in investments in self versus children, as major investments in self are theorized to occur prior to first reproduction (Stearns, 1992), and are more likely to reflect motivations to switch investment from one child to another. Similarly, earlier ages of *last* birth can be theorized to reflect shifts toward investments in child quality, as age at last birth is a primary means of reducing overall fertility, freeing parents to allocate resources to existing children (Towner, Nenko, and Walton, 2016; for a summary of theories on age at last birth, see Mattison et al., 2018).

In sum, fertility and the timing thereof are key drivers of fitness, affecting population growth and dynamics. Ecological evolutionary demography has provided theories addressing both why fertility is potentially so high in humans (due to our system of cooperative breeding), and why it may display, on aggregate, a negative relationship with wealth and economic development. In each case, the costs and benefits of reproduction must be weighed against competing costs and benefits of growth, maintenance, resource acquisition, and status maintenance and the likely effects of each on both current and future offspring. All else being equal, anything that acts to alleviate the costs of reproduction (e.g. presence of allocarers, wealth) can be expected to increase fertility, while anything that contributes to the costs of reproduction (e.g. physiological and energetic costs, high opportunity costs of children) can be expected to decrease it. More fundamentally, EED does not expect fertility to behave the same way in every context, but anticipates that "fertility schedules should respond to ecological conditions." Indeed, although it is possible to describe a human pattern of fertility in relation to other species, it is probably more accurate to describe human fertility as exceptionally flexible, even under "natural fertility" contexts. Thus, a major impulse in evolutionary ecological demography has been to understand the ecological and individual predictors not only of number of children, but also the timing and cessation of childbearing, including strategies surrounding the timing of reproductive maturity, the timing of childbearing, and how these trade off with investments in oneself and in parenting other children.

Mortality

Mortality is relatively little studied by EED compared to other areas of evolutionary demography. This is despite evolutionary demography — and especially biodemography — making key early contributions to theories and descriptions of human mortality (see Wachter, 2008; Sear et al., 2016 for reviews of this literature). Perhaps because mortality is less readily observed (and more difficult to ask about) than fertility, EED with its emphasis on primary data collection in small-scale societies has engaged somewhat less with this core area of demography. Yet, mortality is central to understanding the evolution of human longevity (Hawkes, 2004; Kaplan and others, 2000) and more general patterns of life history (e.g. Charnov, 1991; Charnov and Berrigan, 1993; Ellis and others, 2009); thus, increasing research efforts in the evolutionary ecology of mortality would help to shed light on both general and site-specific causes and consequences of mortality (Burger and others, 2012). Here, we describe how EED has contributed to (1) understanding the basic pattern of human mortality, both in terms of contemporary variation and as it likely evolved over the last 200,000 years, (2) understanding how mortality reflects parental investment in children, and (3) describing how mortality can act as a predictor of variation in human life histories.

The Human Mortality Pattern

An early debate surrounding the human lifespan involved establishing a baseline, ancestral pattern of mortality. The Hobbesian view of a nasty, brutish and short human life had several proponents, including paleo-anthropologist Henri Vallois, who claimed that, among humans, "few individuals passed forty years, and it was only quite exceptionally that any passed fifty" (Vallois, 1961: 433; see also Weiss, 1981; Gurven and Kaplan, 2007). Indeed, evolutionary demographers previously believed that Paleolithic humans experienced life expectancies of only fifteen to twenty years (Cutler, 1975; Weiss, 1981). Such inferences were supported by prehistoric life tables built using osteological evidence recovered at sites such as the Libben site in Ohio (Lovejoy and others, 1977) and Indian Knoll in Kentucky (Herrmann and Konigsberg, 2002) where recovered remains revealed low infant mortality and high adult mortality. These mortality profiles were attributed to "immunological competence" acquired in childhood in small populations subjected to durable pathogenic environments (Lovejoy and others, 1977). Average life expectancies are also relatively short in chimpanzees under diverse ecological conditions (Hill and others, 2001; see also Muller and Wrangham, 2014; Emery Thompson and others, 2007; Wood and others, 2017), although it is reasonably common for individual chimpanzees to live beyond their reproductive years (Emery Thompson and others, 2007). Evidence from Neanderthals, the only other hominin to live contemporaneously with modern humans, lived for rather short durations on average (see Trinkaus, 1995), providing additional support for the idea that ancestral lifespans were significantly shorter in the human evolutionary past.

Yet life tables reconstructed based on data collected, sometimes prospectively, in diverse contemporary hunter-gatherer populations forced a revision of the foregoing view. Such data suggest that the mortality pattern that is characteristic of our species is well described by a Siler distribution (Gurven and Kaplan, 2007; Siler William, 1979; Gage, 1989; Wood and others, 2002) (Figure 3), in which mortality decreases sharply from infancy through childhood, remains more or less constant into middle age, and then rises steadily into old age in "Gompertz fashion" (Gurven and Kaplan, 2007: 322). Based on analysis of demographic data from foraging and foraging-horticulturalist communities, Gurven and Kaplan (2007) conclude that despite high mortality and significant variation across populations, a considerable fraction of humans would have lived to middle age and into post-reproductive periods even under the most stressed conditions. "For groups living without access to modern health care, public sanitation, immunizations, or adequate and predictable food supply, it seems that still at least one-fourth of the population is likely to live as grandparents for 15–20 years." (p. 331) Indeed, Gurven and Kaplan (2007) helped to establish the slow rate of senescence in humans as a distinctive feature of human mortality profiles. Taken together, this evidence contributes to the EED view of longevity as a crucial evolved feature of the human life history (Gurven and Kaplan, 2007; Konigsberg and others, 2006), in which large-scale cooperation among individuals results in decreased mortality and frequent non-reproductive contributions to fitness (cf. Hamilton, 1966) that are focused instead on intra-familial transfers of resources and care (Lee, 2003; Kramer, 2010; Hawkes, 2004; Peccei, 2001; Kaplan and others, 2000: 200).

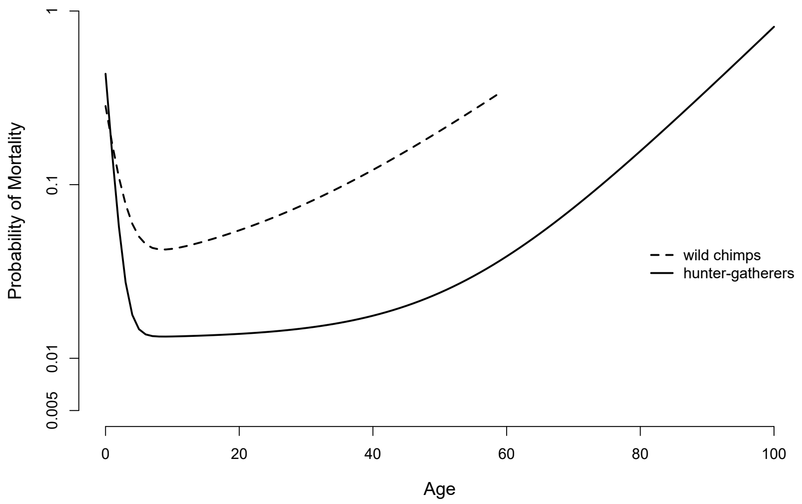

Figure 3. Characteristic mortality in humans and chimpanzees is described well by a Siler distribution and is similar in profile across these taxa, but humans have considerably lower mortality overall, and live for correspondingly longer.

Mortality Is a Proxy of Parental Investment

An obvious implication of the EED view of extended longevity in the context of cooperative breeding is that mortality is a reasonable proxy of inputs into child growth and development. Indeed, cooperative breeding is an enduring focus of work in human behavioural ecology, and probably the most common use of mortality data in EED is for testing hypotheses related to parental (and alloparental) investments in children. Parental investment theory (Trivers, 1972) stipulates that parents will invest in offspring to maximize parental reproductive success, and that such investments will be biased according to their children's ability to convert a unit of parental investment into reproductive success. Thus, son-biased parental investment is thought to pay off when sons are better able to translate investments into reproduction (e.g. due to polygyny; see Sieff, 1990) and investments in a single heir to pay off when a more even distribution of resources leads to lineage failure (Hrdy and Judge, 1993; see also Johowa and others [n.d.]). Variation in mortality can serve as a marker of non-parental investment in children as well. Mattison and colleagues (Mattison et al., 2015; Mattison et al., 2018) explored differences in mortality in adopted versus biological children in colonial-era Taiwan as a test of kin-selection theory to see whether adopted daughters were neglected compared to biological daughters and therefore subjected to higher age-specific mortality (they weren't). General tests of cooperative breeding hypotheses frequently use vital status to infer levels of allocare from different sources (Sear and Mace, 2008). Survivorship has further been used to evaluate quality-quantity trade-offs in human populations (see Lawson and others, 2012), again reflecting the assumption that increased investment into fewer children leads to higher rates of survivorship.

This also serves as a reminder that natural selection may often favour *neglect* of children. Such neglect can range from the extreme (e.g. infanticide, abandonment) to the subtle forms of neglect that most people with siblings will claim to have been subjected to during their childhoods (Hrdy, 1992, 2009). Indeed, while rarely beneficial to a given child, parental neglect may often be optimal for parents, especially in cases where children are insensitive to parental inputs (Caro and others, 2016).

Mortality Predicts Life History Variation

Mortality provides insights as both an outcome variable and as a predictor of demographic behaviour. Major sources of mortality for humans in the course of our evolutionary history and small-scale societies include malnutrition, infectious and parasitic diseases, and conflict with other humans (Gurven and Kaplan, 2007; Gurven and others, 2007; Hill and others, 2007). Yet, as described above, ecological evolutionary demographers have influentially argued that humans have achieved major reductions in mortality compared to apes via increased cooperation through food sharing and alloparenting/cooperative breeding (Kaplan and others, 2000; Kramer, 2010). This has implications for the timing of life history stages across the lifespan.

One influential hypothesis links variation in extrinsic mortality — sources of mortality that are relatively insensitive to adaptive decisions of organisms (Stearns, 1992:182) — to differences in the progression of life histories within and across populations. According to this argument, organisms in high-mortality environments discount the future and prioritize immediacy (Pepper and Nettle, 2013) to capitalize on fitness opportunities earlier in life because a high probability of death means that reproduction is likely to be curtailed (Daly and Wilson, 2005; Ellis et al., 2009; Charlesworth, 1994; Promislow and Harvey, 1990). Similarly, harsh environments generally favour offspring quantity over quality as a bet-hedging strategy to increase the probability that at least some will survive long enough to reproduce (see Einum and Fleming, 2004; Ellis and others, 2009 for a discussion of conservative versus diversified bet-hedging). By contrast, slower life histories are favoured in environments that are predictable, not harsh, but competitive (e.g., Kaplan, 1996), because the rewards of investing in growth and the accumulation of skills and resources are likely to pay off as the future appears more secure and as competition for resources and mates among conspecifics intensifies (Ellis and others, 2009). Cross-cultural evidence supports these general expectations — age at menarche and age at first birth occur approximately one year earlier for every 10% decline in child survivorship to age 15 (Walker and others, 2006; see also Wilson and Daly, 1997; Low and others, 2008) and small body size and early fertility peaks are observed in contexts with high mortality rates (Migliano and others, 2007).

An interesting corollary of hypotheses focused on extrinsic mortality are a group of "socialization" hypotheses that link the quality of parental investment and childhood environments to rates of development. The idea here is that the quality of parental investment serves as a mechanism by which children receive information about the levels of stress and support in local environments, including extrinsic mortality and morbidity (Belsky and others, 1991; Bereczkei and others, 2000; Chisholm and others, 1993; Ellis, 2004; Pepper and Nettle, 2017; reviewed in Ellis and others, 2009). Children reared in environments with low levels of parental investment are thought to cue in on these indicators during childhood to predict future environments and will adjust their life history strategies to accommodate harsh and/or unpredictable environments. Individuals reared in environments with cues of harshness and/or unpredictability — e.g. low socio-economic status, frequent residence or parental transitions — experience faster life histories, including earlier sexual debut, more sexual partners, and earlier age at first birth (see Ellis and others, 2009, for review, and Baldini, 2015, for a critique; see Pepper and Nettle, 2017, for a more recent review and theoretical treatment). This theory has major implications for understanding reproductive behaviour that is otherwise deemed “pathological” according to a public health perspective, and for the interventions employed to decrease the frequency of the early onset of reproduction (Draper and Harpending, 1988; Belsky and others,1991). For demography, it goes beyond standard demographic transition theory to link mortality to reproductive behaviour and attendant psychological mechanisms.

Future EED Work on Mortality

Several interesting questions remain to be addressed by an ecological evolutionary demographic perspective on mortality. Firstly, a question that continues to inspire significant interest in mainstream evolutionary demography involves whether there are limits to extensions of the lifespan (e.g. Oeppen and Vaupel, 2002; Tuljapurkar and others, 2000; Dong and others, 2016). Much of the answer to this question depends on the extent to which existing causes of mortality decline can be applied in forecasting future mortality decline. Burger et al. (2012) note that much of the exceptional decline in human mortality has arisen within only the last four generations and that the difference between contemporary mortality in industrialized populations and that of hunter-gatherers is much greater than the difference between hunter-gatherers and chimpanzees. This, in conjunction with significant contemporary variability in human mortality profiles between populations, may suggest that different factors are at work now compared to the factors operating to lower mortality in our evolutionary past. Indeed, whereas widespread sharing may have reduced deaths associated with famine and malnutrition, most deaths in contemporary hunter-gatherer populations are apparently due to infectious disease, especially post-contact, with additional mortality due to degenerative diseases and, in some groups, homicide. The contributions of modern healthcare and sanitation to declining mortality may extend the human lifespan much further than sharing (Burger and others, 2012); if such extensions facilitate ongoing downward inter-generational transfers, the implications for fitness are very different than if transfers to support longevity move in the other direction (Lee, 2013; Cyrus and Lee, 2013).

Secondly, an interesting question surrounds the extent to which fertility trades off with mortality and the types of evidence that may be used to evaluate such trade-offs. Studies exploring this issue are generally equivocal due to the difficulties associated with assessing the costs of reproduction (Gurven and others, 2016). An intriguing recent study provides evidence supporting such a trade-off in Utah where women’s lifespans were more strongly lengthened following demographic transition than were men’s, whose costs of reproduction were less affected (Bolund and others, 2016). More generally, if fertility is a determinant of mortality, then its effects must be controlled in analyses of mortality. If the costs of reproduction are easily borne by contemporary women (e.g. because their nutritional inputs are sufficient to sustain high fertility or because fertility is low in most modern contexts), then mortality may be relatively immune to the effects of fertility. More empirical data testing this association are needed. Finally, and much more generally, although evolutionary demography was best known early on for its work on mortality (Wachter, 2008; Sear and others, 2016), this area of scholarship has not kept pace with work on the evolutionary ecologies of fertility, which have dominated work in modern EED. Evolutionary ecological demography stands to contribute much to this core area of demographic study.

Migration

Migration is a fundamental driver of evolutionary and demographic change, and a key component of the balancing equation in demography. While the topic is extensively studied by mainstream demographers, it has more rarely been the focus of evolutionary analysis. Yet there has been important work in this area in ecological evolutionary demography. As discussed below, much work has modelled the decisions of adults to disperse from the natal community in terms of costs versus benefits of staying versus leaving. Other work focuses more closely on "post-marital residence", i.e. the decisions made by couples over where to reside after establishing a reproductive union (Stone, 2014). Post-marital residence is highly variable in human societies (Mattison, 2019), from couples remaining in their natal communities (i.e. natalocality), to moving in with or close to the husband's kin (virilocality), to moving in with or near to the wife's kin (uxorilocality). Whether an individual disperses to a new area or stays in their natal community is relevant to key evolutionary questions of mating effort and parental investment, including access to and competition over mates and resources. Drawing from the perspectives of life history theory and the evolutionary study of territoriality, much research has examined the costs and benefits of remaining versus dispersing in different contexts with the goals of understanding when the balance is tipped in one direction or the other and how such decisions affect downstream health and demographic behaviour.

Ecological evolutionary demography provides models of dispersal decisions that unify many disparate costs and benefits (Emlen, 1995; Koenig and others, 1992). Fitness costs of dispersal range from energy, time and risk (of injury, disease, hunger, hostile people or dangerous animals in novel territories) to loss of access to nearby kin (Wood and Marlowe, 2011; Hill and others, 2011). Benefits to dispersal include the fitness benefits associated with control of new territories and associated resources (Hamilton and May, 1977) and mating opportunities (Clarke, 1993), and the reduction of inbreeding risk (Moore, 1993). Finally, scholars have recognized distinct benefits of remaining in the natal territory, including benefits derived from knowledge of local resources and risks as well as increased potential for kin investment and transmission of social information from known community members. As described below, the relative costs and benefits of staying versus leaving are predicted to differ systematically for males versus females, by age and by birth order. In humans, institutions that ratify inheritance can further constrain dispersal decisions (e.g. Clarke, 1993; Clarke and Low, 1992; Koenig, 1989; Strassman and Clarke, 1998; Towner, 2001, 2002). Access to resources has played a correspondingly large role in shaping human dispersal patterns.

Sex-Biased Dispersal

Ecological evolutionary demography has provided key insights into the role that subsistence plays in driving patterns of sex-biased dispersal. Whereas much of mainstream demography views sex-biased dispersal patterns as products of cultural institutions regulating marriage, EED pushes the causal arrow back to viewing these institutions as products of natural selection (Sear, Mattison, and Shenk 2024). For example, different ecologies are predicted to favour male versus female (or relatively egalitarian) control of resources, which, in turn, drives male versus female kin to reside together (e.g. Jordan and Mace, 2007; c.f. Alesina and others, 2013). In general, ecologies with economically defensible resources favour territoriality and group defence (Dyson-Hudson and Smith, 1978; Cashdan and others, 1983; Mattison and others, 2016b). When the resource base becomes productive enough that male reproductive success is more significantly enhanced by resources than is female reproductive success, kinship systems become more male-oriented and virilocality can ensue. Thus, many human subsistence systems, especially those emphasizing the inheritance of land in intensive agricultural systems (e.g. Goody, 1976; Shenk and others, 2010), are characterized by resource defence (Alvard, 2003) and show patterns of either female dispersal (i.e. virilocality) or (typically male) unigeniture (e.g. Boone, 1986; Goody, 1976; Hrdy and Judge, 1993; Murdock, 1967). On the other hand, subsistence systems characterized by horticulture, expansive recourse bases or male absence (e.g. due to fishing) are often uxori- or nata-local, with female kin organizing subsistence efforts (e.g. Mattison, 2011; BenYishay and others, 2017; Alesina and others, 2013; Holden and Mace, 2003). Finally, hunting and gathering are often associated with flexibility in dispersal, with spouses moving between locations strategically over the life course in ways that maximize cooperation among kin as opposed to resource defence (e.g. Wood and Marlowe, 2011; Kramer and Greaves, 2011).

Ecological Constraints on Dispersal

Human dispersal decisions are contingent not just on the subsistence system and related inheritance practices, but also on individual resource-related conditions such as the wealth and status of both self and parents (Goody, 1976; Low and Clarke, 1991; Mace, 1996; Voland and Dunbar, 1995). Such considerations are formalized by the ecological constraints model of delayed dispersal (Emlen, 1995; Koenig and others, 1992; Strassman and Clarke, 1998), which suggests that when offspring have access to cooperative breeding opportunities or improved territories at home, they may delay dispersal either because (a) they will achieve greater fitness benefits (at least temporarily) from serving as helpers at the nest (i.e. by helping to improve parental fitness (Turke, 1988)) in a good breeding territory or agricultural estate, and/or (b) with the hope of inheriting the breeding territory or agricultural estate from their parents. Emlen (1995) has argued that many aspects of the organization of the family across species rest on the principles of inclusive fitness theory, ecological constraints theory and reproductive skew theory acting in concert, with the benefits of cooperation with relatives trading off with competition for resources and reproduction, in explaining the composition and longevity of family groups as well as the age and sex characteristics of dispersers. More specifically, ecological constraints on the resources needed for reproduction (e.g. Koenig and Mumme, 1987), in combination with the benefits of staying in the natal territory under such conditions (e.g., Stacey and Ligon, 1991), have been argued to lead both to reproductive delay and, as a consequence of such delay, to the formation of extended family units (Emlen, 1994, 1995).

Fundamental to the ecological constraints model is the lack of superior alternatives away from the natal household. Interestingly, if the opportunity costs of leaving are low, then many of the factors that are associated with delayed dispersal in the context of ecological constraints lead to dispersal in the absence of such constraints. For example, non-heirs — especially those born at higher birth orders, in larger families or in areas with harsher ecological conditions — are more likely to benefit from dispersal than children with lower birth orders, who reside within smaller families or who are formally appointed as heirs (Boone, 1986; Clarke and Low, 1992; Hrdy and Judge, 1993; Voland and Dunbar, 1995). The likelihood of dispersal among humans peaks in the late teens and twenties (Clarke and Low, 1992; Castro and Rogers, 1984) across cultures. Childless and unmarried people — the same categories of individuals predicted to have the lowest opportunity costs of caring for siblings (e.g., Kramer, 2005) — are more likely to disperse than married individuals or individuals who have children, because these categories of individual will benefit more from additional opportunities to secure mates or the resources necessary to start a family (Glover and Towner, 2009; Strassman and Clarke, 1998; Towner, 2002, 1999).

Push and Pull Factors

The ecological evolutionary perspective focusing on the costs and benefits of dispersal (and as a corollary the costs and benefits of natal philopatry) parallels the discussion of push and pull factors in the study of migration among demographers. Push factors are the reasons that motivate people to leave one community (e.g. poor job prospects, land saturation, high mortality rates) and pull factors are the reasons that motivate people to move to a new community (e.g. good job prospects, access to land and better health care) (e.g. Schoorl and others, 2000; Massey and others, 1994; Jedwab and others, 2015). Most of the work on dispersal in EED focuses on these motivations, providing a link to the literature in mainstream demography. Yet there has been less attention among human evolutionary demographers to recent and ongoing patterns of rural to urban migration and international migration from the developing world — a central focus of migration scholarship in mainstream demography (see Mace, 2008). This will inevitably affect demographic studies of small-scale populations (Neill, 2007; Mattison and Sear, 2016), however, and theoretical links between urbanization, risk, fertility and parental investment (Hrdy, 1992; Mace, 2008) suggest a productive nexus for theoretical and empirical work in ecological evolutionary demography. Gillian Bentley and colleagues, for example, have examined the impact of growing up in Bangladesh vs. in the UK on reproductive function among women of Bangladeshi origin through the lens of life history theory, arguing for a critical period of environmental sensitivity during childhood. They found that growing up in the more stressful environment of Bangladesh (in terms of nutritional stress and exposure to infectious disease) was associated with lower allocations to reproductive effort in terms of progesterone levels (Mora and others, 2007) and ovarian reserves (Begum and others, 2016), but not in terms of levels of estradiol (Núñez-De La Mora and others, 2008) or age at menopause (Murphy and others, 2013). Such insights are important when considering how to extend the demography of small-scale societies within the contexts of migration, where characteristics of sending populations may suggest different interventions into health and well-being for migrants than those employed as standard in receiving populations.

Additional topics that are of central importance to understanding ecologies of migration, if somewhat peripheral to ecological evolutionary demography, include the genetic signatures of migration, which have been used to map the journey out of Africa onto humans' contemporary global distribution. This work has taken many dimensions, including tracing the timing and route of the migrations through archaeological and genetic markers (e.g. the many articles in Crawford & Campbell, 2012 and Cavalli-Sforza et al., 1994), with some arguing that there has been selection among humans for alleles that favour expansion or migratory behaviour under conditions of resource surplus (e.g. Harpending and Cochran, 2002). While many mainstream demographers do not share the interest of anthropologists in the ancient human past, understanding these patterns creates a baseline for understanding policy-relevant types of human migration in the contemporary world and recent past. Another exciting perspective that will add to our broader understanding of human migration derives from cultural evolutionary theory, which has been particularly interested in the effects of migration on social learning processes. For example, unlike its effects on population structure, migration need not erode between-group cultural variation as acculturation to local norms and customs can serve to maintain barriers (Mesoudi, 2017). Similarly, social assortment prevents acculturation and has interesting implications for the maintenance versus erosion of cooperation within groups (Mesoudi, 2017; Boyd and Richerson, 2009) and the likelihood of large-scale demographic events such as warfare (Divale, 1974; Macfarlan and others, 2018; Mathew and Boyd, 2011; Richerson and Boyd, 1998). This work has direct relevance to mainstream demographers interested in diffusion models of behaviour, and also to the patterns and pace of the demographic and social assimilation of immigrants into host populations.

In sum, ecological evolutionary demography has much to contribute to understanding migration decisions. Although historically focused on specific decisions surrounding marriage and family-building, the ultimate rationale provided by evolutionary theory is poised to provide a unifying model of the push and pull factors that have elsewhere been described to affect migration decisions in other contexts (e.g. labour migration). Because migration affects access to resources and social support, it has important consequences for the key drivers of human decision-making, affecting all realms of interest for human behavioural ecologists (Winterhalder and Smith, 2000).

Concluding Thoughts: Key Insights, Limitations, and New Directions

In the quarter century since Low, Clarke & Lockridge (1992) published their article defining the field of ecological evolutionary demography, we have learned much about how individual-level constraints and differences in socio-ecologies affect fertility, mortality and migration. Key topics addressed by this work include resolving both why humans have, as a species, higher fertility than expected based on our long life histories, and why fertility has dropped in association with the demographic transition. The field has also described the basic pattern of human mortality and the reasons our mortality is so low, as well as its interlinkages with other core topics within demography (e.g. fertility and the lifespan). Ecological evolutionary demography has engaged somewhat less with migration studies, but ecological constraints theory and optimization approaches are poised to unify the disparate factors known to affect the decisions of whether, when and where to migrate. In our review of this material, we have touched on several limitations or fringe topics that we believe will be important to revisit as the field continues to grow and strengthen. We draw attention to those here and offer additional suggestions that aim to further integrate ecological evolutionary demography with other core areas of the wider field of evolutionary demography.

A fruitful pathway for integrating the various subfields of demography, including evolutionary demography, is to begin to bridge more systematically the proximate-ultimate division that characterizes much of the current scholarship. An emerging area with good potential to do this involves the study of psychological mechanisms underlying fertility decisions (McAllister and others, 2016; Pepper and others, 2016; McAllister and others [n.d.]). For example, desired family size, including both what happens when you surpass your desired fertility (Mcallister and others, 2012), as well as the "unmet need" or unfulfilled desire for children in post-demographic transition contexts (Testa, 2007), when mothers don't have as many children as their stated fertility desires (Kaplan and others, 2003), are usefully studied from an evolutionary perspective and address key questions in the mainstream demography of fertility. Likewise, much of the work in cultural evolution of fertility describes the uptake of contraception through social networks and in relation to individual circumstances (Colleran and Mace, 2015; Alvergne and others, 2011; Colleran, 2016). Although there is significant debate about whether cultural evolutionary theory is better described as proximate or ultimate (e.g. Laland and others, 2013; Bateson and Laland, 2013), this may actually position it quite well for linking these two perspectives in relation to the mechanisms driving fertility decisions, as well as the adaptive value and long-run dynamics of demographic behaviour.

Various intersections between core areas of demography provide additional scope for extensions of traditional realms of inquiry into more complex understandings of human demographic behaviour. As alluded to above, the feedbacks between fertility and mortality create one nexus that will shed light on demographic behaviour in the past, present, and future. For example, the Neolithic transition, which was accompanied by global shifts toward agricultural and sedentary lifestyles some ten to twelve thousand years ago (Bentley and others, 2009; Bocquet-Appel and Bar-Yosef, 2008; BocquetAppel and others, 2006) is often considered paradoxical, in that increased fertility and mortality were simultaneously thought to have accompanied this transition. Recent scholarship testing key premises of this transition in contemporary small-scale populations transitioning to sedentism have revealed how sedentism can in fact produce the hypothesized effect, with overall increases in fertility despite increased mortality (Page and others, 2016). In particular, cooperative breeding has been key to sustaining high fertility despite increased infectious disease accompanying sedentary lifeways.

There is also interest in the interaction of fertility and mortality, both in our evolutionary past and in the modern world where the average life expectancy for humans has increased "linearly at almost three months per year over the past 160 years" (Gurven and Kaplan, 2007: 321) and women now live almost a third of their lives in a post-reproductive phase. Some findings have shown clear trade-offs between high fertility and mortality, a phenomenon known as maternal depletion, with high fertility being associated with higher mortality in some studies (Gagnon and others, 2009) but not in others, and with reviews of the evidence showing complex results consistent with maternal depletion in some settings, including modern settings (e.g. Hurt and others, 2006; Le Bourg, 2007). More recent work in contemporary high fertility populations suggests, however, that women may often be buffered against trade-offs between health and high fertility, even in high mortality settings (Gurven and others, 2016). An intriguing recent hypothesis suggests that *low* fertility is to blame for the uptick in female morbidity (especially auto-immune conditions) in many contemporary settings (Natri and others, 2019). Much remains to untangle about the relationship between ecology, fertility and longevity in this complex relationship.

Expanding methodologies provides further scope for integration across the subfields of demography. One means by which this is already occurring is via the use of new methods that provide information on proxies of health and demographic behaviour. Central among these are biomarkers that provide information on endocrine and immune function (e.g. McDade and others, 2007; Worthman and Costello, 2009; Valeggia, 2007). The adoption of the use of mobile phones and other devices such as motes (wireless sensing devices) in data collection facilitate tracking of complex social networks (e.g. Page and others, 2017), migratory patterns and other microdemographic data (e.g. disease transmission (Marcel Salathé and others, 2010) that can be challenging to collect via observation or survey. The use of such methods connects ecological evolutionary demographers with practitioners of applied health and demography, showcasing and calling for more work in applied evolutionary demography (Gibson and Lawson, 2014, 2015) and for demographically relevant work in evolutionary medicine and public health (Nesse and Stearns, 2008; Wells and others, 2017). Work in this area has included an explicit focus on population change (Gibson, 2014), family structure and health (Lawson and Uggla, 2014), social disparities in health (Pepper and Nettle, 2017) and nutritional transition (Wells, 2014). A parallel focus on gender and female autonomy has also provided counterintuitive reasons for undesirable social behaviour, including domestic violence (Jones and Ferguson, 2009; Stieglitz and others, 2018), crime and social violence (Schacht and others, 2014; Schacht and Kramer, 2016), dowry harassment (Shenk. 2007), biased sex ratios (Shenk and others, 2014), sex-biased parental investment (Mattison and others 2016a) and the effects of adoption on mortality and investment in children (Mattison et al., 2015; Mattison et al., 2018; Perry, Daly, and Macfarlan, 2014; Prall and Scelza, 2017), and even female genital cutting (Howard and Gibson, 2017). Such insights suggest different targets for intervention by focusing on the evolutionary benefits of socially undesirable behaviours (see also Hill, 1993). Many policy-relevant ideas brought forward by ecological evolutionary demographers simply would not be identified without an evolutionary perspective; such ideas are especially crucial in areas of policy where problems persist, and new thinking is sorely needed. For example, Gibson and colleagues' work on how the installation of water taps affected women in a low-resource setting was informed by life history theory, which highlights how health and fertility are connected. They found an increase in fertility after the installation of this labour-saving technology, which would not have been predicted under standard public health models (Gibson 2014). Equally, EED should consider topics of core interest to mainstream demography, such as the end points of fertility transition and how best to support ageing populations. More generally, these methods and applied topics should open more integrated research, with the potential to reconnect work in ecological evolutionary demography with mainstream demography, as both increasingly emphasize health and improved forms of data collection and population monitoring.

Lastly, even a relatively lengthy overview of ecological evolutionary demography necessarily omits interesting work in areas that don't quite fall within the core of the field. Given the breadth of work in life history theory and parental investment, ecological evolutionary demography provides theory for understanding patterns in many related areas, including the upstream regulators of fertility and spacing behaviour, such as marriage (e.g. Chagnon and others, 2017; Marlowe, 2000), conflicts of interest between the sexes (Leonetti and others, 2007; Moya and others, 2016) and downstream consequences of behaviour, such as social (Mattison and others, 2016b) and health inequality (Pepper and Nettle, 2014). While we have not dedicated the same attention to all of these and many more interesting areas of research, we hope that this review has demonstrated the importance of the ecological perspective to evolutionary demography and, conversely, the usefulness of demographic methods and practice to the ecological perspective. Integration of related methods and theory lies at the heart of the initial founding of the discipline of ecological evolutionary demography (Low et al., 1992). We reiterate here that such integration is critical for recognizing the causes and consequences of well-established demographic patterns, and for identifying new patterns and departures from established theories that may be in need of refinement. In other words, ecological evolutionary demography necessarily comprises threads of diverse disciplines. The task for future work is to interweave these for a fuller and more robust science of demography.

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